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Cotylogaster occidentalis n. sp.
and a Revision of the Family Aspidobothridae.

By

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With Plates 32 and 33 and 1 figure in the text.

The subject of the present paper is a previously unknown representative of the Trematode family *Aspidobothridae* found living in the Mississippi valley. It resembles *Cotylogaster michaelis* Mont. more closely than any other from which is known and I have therefore described it in a preliminary notice (Nickerson '99) as a member of that genus giving it the specific name *occidentalis*. The new form was discovered during the summer of 1899 while upon the house-boat "Megalops" which was maintained by the Minnesota Natural History Survey upon the Minnesota and Mississippi Rivers for the investigation of their fauna. It occurs parasitic in the intestine of the "Sheepshead" *Aplodinotus grunniens* Raf. though by no means abundantly. I found 7 specimens in the intestine of one fish taken from the Minnesota River near Jordan. I have since examined a considerable number of other sheepsheads in the hope of finding more Cotylogasters but without success.

One of the 7 specimens was killed ($HgCl_2$) while flattened in the compressor and subsequently stained and mounted as an entire preparation. This has been of great service in tracing the anatomical relations of the organs as represented in the diagram (Fig. 15). Two of the other 6 specimens were made into serial sections, one series transverse and one sagittal, two were accidentally lost by the evaporation of the alcohol in which they were preserved and the remaining two are deposited as type specimens in the Zoological Museum of the University of Minnesota.

The specimens of *Cotylogaster occidentalis* which I have collected vary in length between 8 and $10^1/_2$ mm. The body (Fig. 1) may be described as consisting of two parts: 1) an anterior, muscular proboscis-like portion forming about one third of the entire length and 2) the body proper comprising the remaining two thirds which is broader, somewhat flattened dorsoventrally and modified on its ventral surface to form the large compound adhesive disk or sucker. The first portion is capable of being retracted telescopically for one half its length into the hinder portion and is expanded at the end into a five-lobed disk having the mouth at its centre. The dorsal median lobe is larger than either of the others and has a pit at its apex from the base of which a papilla rises (Fig. 6). This is probably the seat of a sense organ of some kind and corresponds with the similar structure in *C. michaelis* described by MONTICELLI. The other four lobes are rounded and of nearly equal size. The incision between the two ventral lobes is a little more pronounced than that between any other two. The portion just back of the buccal disk, which may be called the neck, is broader transversely than thick and nearly triangular in cross section (Fig. 8). Its ventral side is nearly flat while the middorsal line is elevated into a ridge rounded on top and slightly concave on the slopes between this ridge and the somewhat thickened lateral margins. Toward its connection with the main portion of the body the form of the neck becomes more nearly cylindrical.

The body proper is nearly elliptical in cross section, the transverse diameter being about $1^1/_2$ mm and the dorsoventral 1 mm. Its posterior end is curled strongly upward in the natural condition of the living worm in all of the specimens. A broad conical elevation, the dorsal cone, rises from the dorsal side near the posterior end; its summit might readily be mistaken for the posterior tip of the body but the presence of the excretory pore posterior to it and also the arrangement of muscles and other internal organs show that it is not such morphologically.

The large ventral shield or sucker covers the whole ventral side of the body and extends up laterally until its edges are nearly as high as the dorsal surface (Figs. 1, 9 and 10). It is a muscular organ containing depressions or acetabula varying in number from about 132 to 144. The whole median portion of the organ is occupied by 31—34 greatly elongated transverse grooves separated by feebly developed transverse partitions or ridges and nearly equaling

in length the transverse diameter of the worm. This series is completely surrounded by a single marginal row of rounded or elliptical depressions varying in number from 100 to 110.

The acetabula of the marginal row show no regularity of arrangement with respect to the grooves of the median series.

Marginal organs are present corresponding in position with those of *Aspidogaster*, *Cotylaspis* and *Cotylogaster michaelis*. Their structure will be described later.

The sexual aperture is median ventral a short distance in front of the anterior margin of the ventral shield when the animal is fully extended (Fig. 2). When the anterior portion is retracted the gonopore is carried backward so as to open into the sulcus surrounding the base of the retratile neck (Fig. 7).

A cluster of deeply staining cells is present in the tissue at the base of each of the marginal depression of the ventral sucker. They are doubtless glandular in function and correspond with the cutaneous glands described as occurring in corresponding positions in several other members of the family.

At the junction of the neck with the body the musculature is reflected inward and backward to form a muscular tube within the parenchyma. This lies near the dorsal side separated from the body-wall by only a thin layer of tissue and extends backward to about the region of dorsal flexure. It is composed of an outer coat of longitudinal fibres, a middle coat of oblique fibres and a few inner circular fibres, finer and less numerous than those of the other two sets. Some of the muscle fibres forming the dorsal side of the tube continue backward across the base of the dorsal cone and are attached at the posterior end in the vicinity of the excretory pore. The tube is larger at its anterior end and there occupies the greater part of the body space but gradually diminishes in size posteriorly (Figs. 7, 9 and 10). Within it are contained the intestine, the longitudinal excretory tubules, and the terminal portions of the oviduct and vas deferens. The other prominent organs, ovary, shell-gland, testes, vitellaria and uterus are contained in the space between the walls of this tube and the ventral and lateral body walls.

As in other *Aspidobothridae* the digestive tract consists of prepharynx, pharynx and simple unforked intestine. The prepharynx extends this the centre of the neck from the mouth back to the pharynx, a distance varying in the three specimens measured, from 0.823—1.48 mm. The average of the three cases is 1.1 mm. Its

oral end is not specially modified in any way. Its lumen is compressed laterally and measures in transverse section about 5×37 μ. Its wall consists of a thin cuticula outside of which is a layer of delicate longitudinal muscle fibres. Circular fibres are lacking. Immediately around the prepharynx (Fig. 8) is a cord of parenchyma in which no muscle fibres are present. This has an elliptical outline in cross-section and extends longitudinally through the central portion of the neck. The strong dorsoventral fibres of the neck musculature border this parenchyma on the sides and probably by their contraction produce the lateral compression which closes the lumen of the prepharynx. At its hinder end the prepharynx enlarges abruptly to unite with the pharynx. This latter organ is nearly cylindrical in form and measures about 0,45—0,55 mm in length. It is however laterally compressed giving an elliptical outline in transverse section measuring about $0{,}26 \times 0{,}315$ mm. Its narrow lumen measures only about 20 μ transversely by 212 μ dorsoventrally. It is situated above and a little in front of the sexual aperture (Fig. 7).

The intestine extends from the pharynx back to the region of dorsal flexure of the body. Its shape undergoes certain changes of outline as seen in transverse section but I have no means of knowing to what extent these changes are due to temporary states of contraction. Figs. A 1—9 show in outline the form and relative size of the intestine at 9 successive points back of the pharynx the last being taken opposite the ovary. Posterior to the ovary the intestine undergoes very little change in size or shape to its abruptly rounded termination. MONTICELLI divides the digestive tract back of the pharynx in *C. michaelis* into two regions oesophagus and intestine. I see no reason for making a similar division in this case as there is no characteristic structural difference between the two parts nor any definite line of separation. I do not see that anything would be gained by making such a division arbitrarily.

The epithelial lining of the intestine is composed of a single layer of cells which show great variation in form evidently due to amoeboid changes. In some regions they appear flattened almost squamous in character in others as greatly elongated cells with their nuclei near the base and with their outer ends projecting into the lumen of the intestine and vacuolated. The epithelium rests upon a delicate basement membrane beneath which is a layer of longitudinal muscle fibres. The outer layer of circular fibres described by MONTICELLI as occurring in *C. michaelis* is represented in *C. occidentalis*

by only a few scattered circular fibres which may occasionally be recognized about the posterior portion of the intestine.

Monticelli has described the intestine of *C. michaelis* as being much enlarged posteriorly to form a varicose sack. It seems extremely improbable that any state of contraction of the body could bring about such a condition of the intestine of *C. occidentalis*. It is much more probable that there is in this respect a real difference between the two forms.

The only food material observed in the intestine was a small number of blood corpuscles.

The opening of the excretory system is at the posterior end of the body just above the edge of the ventral shield and at the base

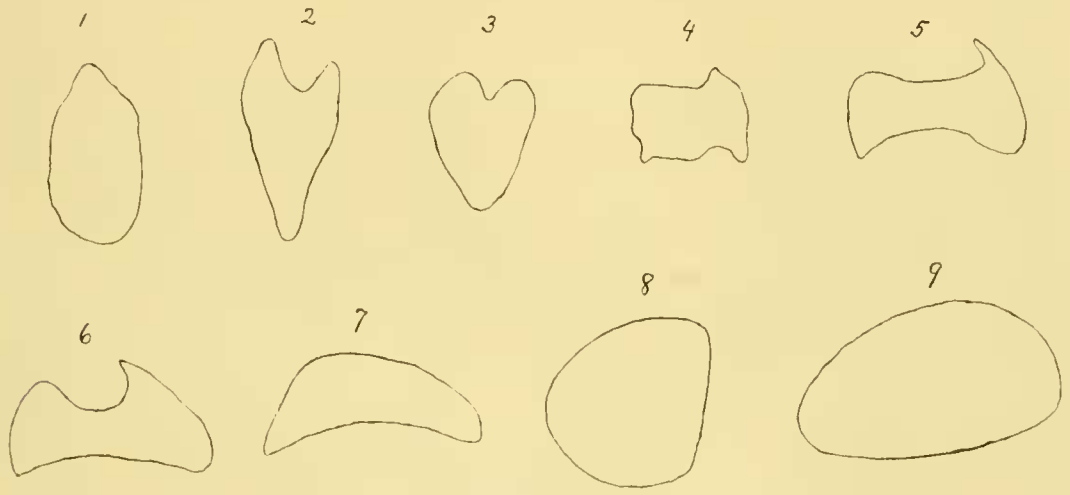

Fig. A.

of the dorsal cone (Fig. 7). There is here an invagination of the body wall forming a tubular depression into the base of which two small pores open laterally, one from each of the two excretory vesicles. These vesicles are extremely thin walled resembling mere cavities in the parenchyma and are quite unconnected with each other. I have not traced the course of the tubules which empty into them. One peculiar feature of the excretory system deserves special mention. An elongated rather deeply staining structure is very clearly to be seen in the total preparation mentioned extending for some distance on either side of the prepharynx just back of the oral disk (Fig. 15 *ex.t*). Sections show this to be a tubule having thick walls containing large nuclei but not showing cell outlines. The lumen of the tubule is irregular in outline and has an average diameter of about 6 or 7 μ. The length of the enlarged portion of the tubule is a little

more than a third of a millimeter. Posteriorly this tubule is continued into a minute very thin walled vessel similar to the excretory tubules usually seen in sections of trematodes. I have been able to follow its course but a short distance. Anteriorly the tubule becomes thin walled but larger in diameter and extends forward and upward into the dorsal median lobe of the oral disk nearly to the tip. Here it turns sharply upon itself and extends backward diminished in size as one of the longitudinal excretory vessels which lead backward to the excretory vesicle. It may safely be assumed that so highly specialized a portion of the system as I have described is of functional importance though in what way is at present open only to conjecture. No such modification of the excretory system has been reported of other Aspidobothrids nor so far as I know of other trematodes.

There appears to be a difference between the two species of *Cotylogaster* also in the position of the excretory pore. In *C. michaelis* it is according to MONTICELLI at the summit of the dorsal cone; in *C. occidentalis* I find it at the base of the cone. The surface appearance of the latter form strongly suggests an aperture at the apex of the cone (Fig. 5) tho' sections show that the aperture is really elsewhere. A comparison of MONTICELLI's fig. 1, tab. 22 with my Fig. 7 leads me to suspect however that the difference in the position of the aperture in the two forms is really not so great as appears from the descriptions. It appears very questionable whether the dorsal cone "conischen oder cylindrischen Zapfen" mentioned by JÄGERSKIÖLD ('99, p. 202—203) as occurring in *Macraspis* can be considered homologous with that in *Cotylogaster* since JÄGERSKIÖLD's fig. 5, p. 202 shows that not only the caudal foramen but also the posterior end of the intestine and the rudimentary sexual organs are contained in it.

No satisfactory description of the nervous system of *C. occidentalis* can be given as the brain and nerve trunks are very obscure in the sections and so not favorable for observation. The brain corresponds in position with that of *C. michaelis* lying above and at the sides of the prepharynx just back of the oral disk and ventral to the thick-walled excretory tubules previously described. The nerves leading from it I have not followed. The study of my sections has given however some interesting facts concerning the peripheral nervous system as represented by the marginal sense organs of the ventral sucker. These organs have been reported as occurring in all the

genera of this family except *Stichocotyle* [1]). They are however probably larger and more favorable for investigation in *C. occidentalis* than in either of the other members of the family in which they have been observed. The bulb of the one represented in Fig. 11 measures 38 × 27 μ and the total length from the base of the organ to its opening at the surface 55 μ. They correspond in position with the similar organs of *Aspidogaster*, *Cotylaspis* and *Cotylogaster michaelis* lying at the margin of the sucker one in the outer end of each septem between the marginal alveoli. The body of the organ is ovoidal in shape and is connected with the exterior by a narrow tortuous duct. Starting from the outer end of the bulb the duct bends sharply downward by its side and then makes a second turn toward the surface of the body where it opens (Fig. 14). The organ is limited by a delicate membrane outside of which is a layer of fibrous tissue and the parenchyma. The duct to the exterior has the same coverings and its terminal portion is lined by a cuticula directly continuous with that covering the body of the worm. This ends abruptly about one third of its length inward from the surface (Fig. 11).

The interior of the bulb is made up of a material which differs markedly in different organs ranging from a coarsely vesicular to a finely granular condition (cf. Figs. 11—14). This I interpret as the cytoplasm of glandular cells in different states of activity notwithstanding the fact that no nuclei are discernible in it, with the exception of nuclei of nerve cells to be described later. In the absence of visible nuclei it is impossible to say whether each organ is made up of one large glandular cell or of several. At the deeper end of the bulb the sheaths are pierced by a bundle of delicate fibrous material which in some cases can be traced back through the parenchyma for a considerable distance and is without doubt a bundle of nerve fibers. Its size would indicate a very strong innervation of the organ although by the method employed ($HgCl_2$-Iron-Haematoxylin) nothing could be learned concerning their ultimate distribution. In many cases a number of bipolar cells are clearly shown entering the side of the organ next the convoluted portion of the duct and extending for short distances apparently along the surface of the gland cells. These I regard as undoubtedly sensory nerve cells though the exact method and place of their termination could not be made out. The fact that they are always on the side of the organ

1) List of genera on page 612.

next the duct is probably significant of some relation to it. Sensory cells have not been demonstrated in the marginal organs of other members of this family.

A condition of the organ observed in only one case is shown in Fig. 13. The terminal portion of the duct is everted and the interior of the body of the organ is protruded tho' the opening to the exterior. VOELTZKOW ('88) observed that the marginal organs of *Aspidogaster* were capable of protrusion and retraction and upon this fact based his conclusion that the organs are sensory in function. It is possible that the protrusion of the organ aids both in the exercise of its sensory function and in the discharge of its secretion. The study of these organs with the aid of intra vitam methylen blue staining would doubtless show many details of the nervous structure which it is quite impossible to make out by ordinary stains used upon preserved material. They offer an interesting field for investigation by this method when the necessary living material can be obtained.

In Fig. 12 I have also represented a peculiar condition observed only in the case shown. Immediately beside the duct of the organ figured lie two vesicular structures closely in contact and hyaline and unstained. I can offer no explanation of their presence.

It is a fact of some interest in this connection that in the two closely related genera *Cotylogaster* and *Cotylaspis* the marginal organs which must unquestionably be regarded as strictly homologous differ markedly in structure. Through the courtesy of Prof. H. L. OSBORN I have been permitted to examine his sections of *Cotylaspis* and he has stated to me his conclusions [1]) concerning the structure of these organs. It would appear from VOELTZKOW's description that the organs of *Aspidogaster* resemble those of *Cotylogaster* more closely than those of *Cotylaspis* though it is perhaps probable from general anatomical features that *Cotylaspis* and *Aspidogaster* are more closely related than are *Cotylogaster* and either of the other two forms. Not enough is known concerning the marginal organs of *Macraspis* (JÄGERSKIÖLD '99) to enable a comparison with them to be made. *Stichocotyle* lacks these organs.

It is perhaps probable that the tentacles described by MACDONALD ('77) from the ventral shield of *Aspidogaster macdonaldi* will

1) To be published in a forthcoming number of the Journal of Morphology.

prove to be only highly developed marginal sense organs homologous with those of other Aspidobothrids and capable of protrusion and retraction in a manner similar to those which I have described.

The chief organs of the reproductive system, ovary, testes, vitellaria and shell gland lie ventral to the inner musculatur tube and in a general way resemble those of *C. michaelis* with the right and left relations reversed. The ovary has nearly the form of a prolate spheroid with its longer axis longitudinal. It lies at the right of a median plane, nearer the dorsal surface, over a point about one third the length of the ventral shield back from its anterior edge. It is, in the specimens studied, a very little smaller than the testes, the longer axis measuring nearly 0.5 mm. The shorter axes are a little more than half as long as the major. The relations of the ovary and the complex of organs in intimate relation with it are expressed somewhat diagrammatically in Fig. 16. The oviduct arises from the left (mesial) side near the posterior end and extends forward along the side of the ovary, arching to the right across its anterior end. Then after giving off LAURER's canal it turns rather sharply to the left toward the shell gland. From the mouth of LAURER's canal to the shell gland the tube is ciliated but no cilia are discernible between the ovary and the opening of LAURER's canal. Projections of the wall of the duct are present however in this portion extending obliquely into the lumen at short intervals with their free edges directed away from the ovary. They give in longitudinal sections of the duct an appearance suggestive of the spiral value in the intestine of the selachian. From 12—15 of these projections are present on each side, as seen in longitudinal section, those from the opposite sides appearing to be neither strictly opposite nor definitely alternate in position.

This modification of the proximal part of the oviduct probably corresponds essentially with that described by VOELTZKOW ('88) and STAFFORD ('96) in *Aspidogaster*. Prof. OSBORN informs me that he has observed the same condition in *Cotylaspis*. These three are however the only members of the family in which it has been reported. LAURER's canal communicates with the oviduct by a narrow opening but at once widens out into a rather broad cavity filled in my longitudinal series with an aggregation of spermatozoa. It follows the dorsal surface of the ovary backward becoming narrower posteriorly and opposite the hinder end of the ovary is deflected ventrally into line with the major axis of that organ. From this point it continues caudad

in a generally straight course to the region of dorsal flexure where it bends upward. It opens into the tubular depression at the posterior end of the body already described as receiving the openings from the two excretory vesicles. The opening of LAURER's canal is median, between those from the excretory vesicles, and from the anterior or dorsal side. This method of opening to the exterior in common with the excretory system is peculiar the only similar case with which I am acquainted being one described and figured by Looss ('99, fig. 71, tab. 30) and occurring in an Egyptian species of *Urogonimus*.

Both MONTICELLI ('92) and BRAUN ('89—'93) in giving the characteristics of the family *Aspidobothridae* state that LAURER's canal is absent. Yet VOELTZKOW ('88) described as a "receptaculum vitelli" a structure in *Aspidogaster conchicola* which BRAUN recognized as a modified LAURER's canal. STAFFORD ('96) described the same organ as a LAURER's canal. JÄGERSKIÖLD ('99) states that LAURER's canal is present in *Macraspis*. With my discovery of its presence in *Cotylogaster* it is now known to occur in at least half of the genera comprising the family. This will necessitate a modification of the statement of family characteristics as given heretofore.

The oviduct is joined by the unpaired vitellary duct just before entering the shell gland. The latter organ is situated a short distance anterior and to the left of the ovary in the median plane.

Immediately after emerging from the shell gland the uterus turns caudad and enlarges to form a considerable chamber filled with sperm — the receptaculum seminis uterinum. The part of the uterus following this enlargement is long and tortuous filling most of the space between and around the other organs. It is impossible to follow its windings but the condition of the contained eggs and embryos may be used as a means for determining its general arrangement. Its course as made out by this means is represented in the diagram (Fig. 15). The ova pass backward from the vicinity of the shell gland in or a little to the left of the median line nearly to the posterior end then across to the right side and forward to near the anterior end; here they cross in front of the shell gland to the left side and again backward along that side to the posterior end of the inner muscular tube. Within this they pass forward, the anterior portion of the uterus here lying ventral to the intestine and on the left of the vas deferens. The terminal portion of the uterus (vagina?) is surrounded by a thick sheath of elongated gland cells corresponding with those in *C. michaelis* which MONTICELLI called "glandole glutinipare".

The vitellary gland is a single continuous cord of tissue extending along each side of the body and arching across the anterior end just in front of the shell gland (Fig. 15). Its ends are thicker than the anterior arched portion and reach backward to about opposite the end of the intestine. The unpaired duct arises upon the left side and extends forward to join the oviduct just before the latter enters the shall gland. I have seen no indication of a corresponding duct upon the right side. *Macraspis* is the only other Aspidobothrid in which the vitellaria have been found in the form of continuous bands of tissue (JÄGERSKIÖLD '99); but in that form the connecting anterior arched part is not mentioned and paired ducts are present. All others Aspidobothrids so far as known have the vitellaria in the form of separate rounded follicles arranged in a row along each side. The condition in *Stichocotyle* is not known but it may not improbably be found to resemble *Macraspis* and *Cotylogaster occidentalis* in this respect.

The testes are two in number, elliptical in outline and placed one obliquely behind the other in the middle region of the body. In all of the specimens (3) whose internal structure I have studied carefully the anterior testis is on the right side or (in one case) median while the posterior is on the left side. They are a little larger than the ovary (500—550 × 250—275 μ) and in my specimens are filled with cells showing various stages in the process of spermatogenesis. The ducts leading from the testes (vasa efferentia) arise from their anterior ends but I have been unable to trace them to their point of union to form the vas deferens. The latter organ extends forward thro' the inner muscular tube ventral to the intestine and upon the right side of the uterus. The terminal portion of the vas deferens reaching nearly half way back to the posterior end of the inner muscular tube is enlarged and quite irregular in outline and is surrounded by a thick sheath of elongated gland cells (Figs. 7 and 15). The lumen I have found occupied by masses of sperm and ova, the latter probably drawn backward from the opening of the uterus by some contraction of the body. The vas deferens and terminal portion of the uterus unite just before opening to the exterior so that they have a short terminal portion (genital atrium) in common. A penis is lacking and I can offer no observations to show whether or not cross fertilization occurs.

The eggs in the oviduct before the beginning of cleavage are spherical in form and measure about 26 μ in diameter. The shell of

the uterine eggs is thin and delicate and generally shrivelled in my specimens except in the case of those eggs which were nearly ready to be discharged. These have retained their form and measures about 98×60 μ, the outline being elliptical, the two ends alike, and the line of separation of the lid not evident. I have not traced the development of the embryo but have made some observations upon the fully formed embryos just emerged or ready to emerge from their shells. Sections of such embryos are represented in Figs. 17—21. Fig. 17 represents a nearly sagittal section of an embryo already freed from the shell and contained in the sulcus about the base of the retracted neck (cf. Fig. 9). The oral cup or funnel, the prepharynx, pharynx and intestine are shown already formed and in relations such as may be considered typical of the family *Aspidobothridae*. The large shaded area near the posterior end represents a posterior sucker cut one side of its central depression, the next section (Fig. 18) passing thro' its centre. Above the posterior sucker there is shown in Fig. 18 an oval clear space having somewhat the appearance of a highly vacuolated single cell. Transverse sections show that two such cavities exist side by side. It is safe to assume that these are the rudimentary excretory vesicles.

Fig. 19 represents parts of two adjacent nearly transverse sections thro' the region of the pharynx and shows especially the tufts or clusters of cilia which make here an incomplete band around the embryo. On the ventral side the cilia tufts are lacking. Portions of the same band in other embryos are shown in longitudinal section in Figs. 17 and 21. A comparison of Figs. 20 and 21 will make clear the relations of these tufted cilia. Each cluster arises from a central crater like depression which is enclosed by a circular rim like ridge in which nuclei are present. In the case shown in Fig. 20 there are two nuclei as I have also observed to be case in some other instances but whether more than one are present in all cases I have not determined. Cell outlines I have been unable to distinguish. A cluster of similarly ciliated cells is also present at the posterior end of the embryo as represented in Fig. 17 but I have not determined their exact number.

The cells from which the cilia arise form very evident thickenings of the integument which elsewhere is thin and very nearly homogeneous in appearance. In places however I have been able to distinguish what appear to be very indistinct nuclei in this layer as shown in Fig. 17 (*n*). Their presence together with the absence of

any distinct separation between the cilia bearing cells and the thinner portion of the integument covering the rest of the body have convinced me that the outer layer of the embryo is a modified epithelium as Braun, Monticelli and others have claimed to be the case in trematodes generally. In the adult no trace of nuclei is perceptible tho' we must consider it probable in view of Voeltzkow's observations on *Aspidogaster* that the embryo develops directly into the adult. If this be true the integument of the adult must be regarded as fundamentally a modified epithelium lacking all traces of nuclei and cell outlines. Whether other processes have subsequently occurred to modify this primitive or embryonic condition must remain an open question. The evidence from various sources seems to agree in showing that the integument of trematode embryos is a modified epithelium. I am not convinced however that it is safe to assume as some have done that no additional or supplemental process has operated to produce the often very greatly increased bulk of material in the covering of the adult animal. A reexamination of my sections of larval stages of *Stichocotyle* (Nickerson '95) fails to show any trace of nuclei in the integument. In view of the statement of Odhner ('98) that the adult attains a length of 105 mm, more than 15 times the length of the largest described embryo, it is difficult to understand how such increase of the integument as this necessitates can occur without there being a growing zone somewhere present and I am not acquainted with any biological conception of growth which does not involve the presence and participation of nuclei. The observations of Pratt ('98) upon *Apoblema* (= *Hemiurus* Rud.) seem also to show that another process than obliteration of nuclei and cell boundaries of an epithelium must be taken into account in explaining the conditions in the integument of that form. It seems clear from such cases that there must be a secondary or supplemental process concerned in the formation of the integument of the adult but questions concerning the nature of this process can be answered at present only by hypotheses.

A cluster of large elongated cells represented in Figs. 17, 19 and 21 is present in the anterior end of the embryo. The bodies of the cells lie above the pharynx and send slender processes forward which reach to the surface at the extreme tip of the body (Fig. 21). The number of these cells is small, probably not above four. The cytoplasm is filled with granules which stain with acid dyes (Tropaeolin). The form and relations of these cells together with the condition of the cytoplasm indicate a secretory function. Their number, form and

position render it probable that they are spine glands (Stacheldrüsen) such as occur in larval stages of many *Distomidae.* I have not been able to detect spines in those studied but their absence finds a sufficient explanation perhaps in the extreme youth of the embryos. If my interpretation of these cells is correct their presence gives reason for believing that *Cotylogaster* is like *Stichocotyle* in having two hosts and that it is makes its way into the first of these by the use of spines. I have already suggested it as probable that a similar method of infection of the primary hosts occurs in the case of *Stichocotyle* (NICKERSON '95, p. 478). The conditions in the embryo of *Cotylogaster* not only increases the probability that that suggestion was correct but also suggests the further inference that the Aspidopothrids generally live in two successive hosts, the intermediate host being known only for *Stichocotyle.*

In the middle portion of the body of the embryo ventral to the intestine is a mass of granular tissue containing large nuclei with prominent single nucleoli. It is probably the rudiment of the future sexual organs. Mitotic figures are occasionally seen in these nuclei one such being shown in Fig. 18.

The only other Aspidobothrid embryo available for comparison with that of *C. occidentalis* is that of *Aspidogaster* described by VOELTZKOW ('88). A number of points of resemblance between the two have been alluded to. Their most prominent differences are 1) the absence in *C. occidentalis* of the rudimentary tail which VOELTZKOW described in *Aspidogaster*; 2) the absence in *C. occidentalis* of a distinct oral sucker as described and figured for *Aspidogaster* and 3) the presence of cilia in tufts upon the body of *C. occidentalis* which are absent in *Aspidogaster.*

The latter difference necessitates dropping one of the family characteristics as stated by BRAUN, viz. the absence of cilia upon the developing embryo.

The systematic position of the new worm remains to be considered. I give below (p. 611) in tabular form a statement of the chief differences between it and *Cotylogaster michaelis* as described by MONTICELLI.

Most of the differences mentioned are undoubtedly of only specific value. A few of the others may perhaps be regarded as of sufficient importance to warrant the establishment of a new genus for the form exhibiting them. Such are the differences in the condition of the

	C. occidentalis	*C. michaelis*
Size	8—10½ mm long	4—5 mm long
Buccal disk	5lobed	heart shaped
Ventral shield	132—144 alveoli 100—110 marginal 31—34 median marginal alveoli not arranged regularly with respect to those of median row	70 alveoli 50 marginal 20 median marginal alveoli arranged regularly with respect to those of median row
Ovary	on right side	on left side
Vitellary glands	one elongated continuous cord of tissue arching across anterior part of body and extending back on each side to opposite the end of the intestine	numerous rounded follicles of gland tissue in a linear series on each side and meeting in an arch near the anterior end of the body
Vitellary ducts	single duct on left side	paired ducts, one from each side
LAURER's canal	present, opening near posterior end with excretory pores.	lacking
Penis	lacking	present
Intestine	not much enlarged at posterior end	enlarged to form sack at posterior end
Excretory pore	near base of dorsal cone	at summit of dorsal cone (?)
Eggs	spheroidal 98 × 20 μ long	ovoidal 84 μ long
Habitat	freshwater Teleosts — N. America	marine Teleosts — Mediterranean

vitellary glands and ducts, in the presence or absence of a LAURER's canal and in the presence or absence of a penis. It is possible that such generic separation of the two forms may eventually become desirable but in the present state of our knowledge of the family I consider a conservative attitude in regard to the formation of new genera, the wiser one. I have therefore included this species in MONTICELLI's genus *Cotylogaster* making such modifications in the definition of the genus as given by MONTICELLI and BRAUN as the characteristics of the new form make necessary.

So many modifications of the statement of family and generic characteristics of the several members of this family have become necessary by reason of the additions to our knowledge of them made since the publication of MONTICELLI's revision and BRAUN's classification based upon the latter that it seems best fully to restate the classification of the family. The classification which follows is in no sense a new one but merely such a modification of that given by BRAUN ('89—'93), following MONTICELLI ('92), as is sufficient to incorporate the facts made available since the publication of the pre-

vious classifications. I agree fully with JÄGERSKIÖLD ('99) that it is too early to give a final revision of the family *Aspidobothridae*. That can be done only when more forms shall have become known and the life histories more fully worked out. It is possible as he has suggested that the present somewhat isolated position of the family may have be exchanged for one indicating a closer relationship to the digenetic forms.

I have made no attempt to give the synonymy nor to furnish complete lists of the literature since these are already available in the propers of MONTICELLI and BRAUN up to the time of their publication. The literature lists which I give are intended to include only the propers containing original descriptions and publications which have appeared since the preparation of the bibliography given by BRAUN ('89—'93).

The genera which I recognize as comprising the family *Aspidobothridae* are the following:

Aspidogaster VON BAER (1827)
Cotylaspis LEIDY (1857)
Macraspis OLSSON (1869)
Stichocotyle CUNNINGHAM (1884)
Cotylogaster MONTICELLI (1892)

I recognize five genera as did MONTICELLI tho' but three of these, *Aspidogaster*, *Macraspis*, and *Cotylogaster* are the same as given by him. Moreover it has been necessary to make greater or less change in the definition of each of these genera. The genus *Aspidogaster* remains essentially unchanged except that the form which LEIDY described as *Cotylaspis insignis* and which MONTICELLI included in the genus *Aspidogaster* has been taken out and restored to its position as the type of a distinct genus, *Cotylaspis*, a position to which the work of OSBORN ('98) and KOFOID ('99) has shown it to be entitled. Some changes have been made in the definition of the genus *Macraspis* as the recent work of JÄGERSKIÖLD ('99) has made necessary. The genus *Cotylogaster* has also been slightly modified to include the new form *C. occidentalis*. These changes do not however essentially modify the definitions of these three genera as given in MONTICELLI's classification.

The genus *Aspidocotyle* DIES. I have excluded from the family following in so doing the example of BRAUN (89—93, p. 907) who has placed it among the *Amphistomidae*. So long as nothing more is known

concerning the internal structure of the single specimen representing this genus its systematic position will continue a matter of conjecture. In view however of DIESING's statement (in: Ann. Wien. Mus., V. 2, 1839, p. 234) quoted by MONTICELLI, that the animal has a forked intestine I fully agree with BRAUN that it should not be classed among the *Aspidobothridae*.

The genus *Platyaspis* MONT. I have also suppressed putting the form for whose reception MONTICELLI established this genus in the genus *Cotylaspis*; hence the names *Aspidogaster lenoiri* POIR. and *Platyaspis lenoiri* MONT. become synonyms of *Cotylaspis lenoiri*. KOFOID ('99) while producing conclusive evidence of the validity of LEIDY's genus *Cotylaspis* holds nevertheless that "MONTICELLI's genus *Platyaspis* should for the present at least be retained for the reception of POIRIER's species". As in suppressing MONTICELLI's genus *Platyaspis* I have acted in accordance with a conflicting opinion I will state here some of my reasons for doing so. KOFOID says: "The points of contrast between the two genera (*Cotylaspis* and *Platyaspis*) as described are the presence or absence of eyes, the number of alveoli in the ventral sucker (29 in *Cotylaspis*, 25 in *Platyaspis*) and the ectoparasitic habit of the one and the endoparasitic habit of the other". I am unwilling to concede that either of these three differences is of generic importance. OSBORN's observation that some specimens of *Cotylaspis insignis* are destitute of eyes together with the fact mentioned by KOFOID that "the absence of eyes in *Platyaspis* is inferred from POIRIER's silence upon the subject" make the first difference of very slight value, certainly too small to be made the basis of generic distinction. I regard it as deserving no greater consideration than the presence or absence of marginal sense organs which we know are present in *C. insignis* but know nothing about in *C. lenoiri* since "POIRIER in his original description makes no statement as to the presence or absence of these organs" (KOFOID). KOFOID evidently does not consider this (possible) difference as deserving any consideration since he fails to mention it as one of the "points of contrast between the two genera". I quite agree with him that POIRIER's failure to mention them is no better evidence against their presence than was LEIDY's failure to mention them in *C. insignis* in which form we now know that they are present. I regard their presence in *C. lenoiri* extremely probable.

If a difference in the number of alveoli in the ventral sucker be considered a generic distinction every species now included in the

family *Aspidobothridae* will have to be recognized as a distinct genus. Furthermore every species of which a considerable number of specimens has been carefully investigated has been found to exhibit variation in this respect. Stafford ('96) says of *Aspidogaster conchicola*: "The number of fossettes [= alveoli] varies with the number of transverse ridges which latter increase with the age of the animal. . . . . The greatest number of acetabula that I have counted in the adult is 118." Jägerskiöld ('99, p. 202) says concerning *Macraspis elegans*: "Auf diesem Stadium . . . . ist die Zahl der Saugnäpfe des Bauchschildes ziemlich gering — nur ca. 10. Nach hinten geht aber das Bauchschild ohne scharfe Grenze in ein an Kernen sehr reiches aber ganz muskelarmes Blastem über, das bis zum Hinterrande des Körpers verfolgt werden kann. Es entstehen offenbar aus diesem Blastem die neuen Sauggruben. Diese nehmen somit von vorn nach hinten an Zahl zu. Eine sehr ähnliche Bildungsweise wird . . . . für *Stichocotyle nephropis* beschrieben. An dem grössten und ältesten meiner Exemplare habe ich beinahe 100 Sauggruben zählen können, und doch folgt auf die letzte derselben noch ein kleines Blastem, wie das oben besprochene." Odhner ('98, p. 512) writes of *Stichocotyle nephropis*: "Auf der Bauchseite findet sich eine einfache Längsreihe von Saugnäpfen, deren Zahl je nach der Länge des Wurmes, zwischen 20 und 27 wechselt." In *Cotylogaster occidentalis* I have found the variation in the number of alveoli in the seven specimens examined to exceed the difference said to exist between *Cotylaspis insignis* and *C. lenoiri*. Furthermore I learn from Prof. Osborn that he has found the alveoli in the different specimens of *Cotylaspis insignis* to show a certain amount of variation in number and arrangement. We know that in several Aspidobothrids (*Aspidogaster*, *Macraspis*, *Stichocotyle*) the number of alveoli increases with the age of the animal. We have however no means of knowing that Poirier's specimens were fully adult and that they had attained the maximum number. The differences in the five cases cited are unquestionably only individual differences. I certainly am unwilling to recognize a similar difference between *Cotylaspis insignis* and *C. lenoiri* as of generic importance and should consider it unwise in any case to select as the basis of generic distinction so variable a character as the number of alveoli in the ventral sucker has been shown to be.

The third point of difference which Kofoid mentions — in habit — I regard as somewhat less than the use of the terms ecto- and endoparasitic immediately suggest; for though the interior of the

mantle cavity of members of the *Unionidae* is morphologically the exterior of the body I think we can hardly regard the conditions surrounding *Cotylaspis* in the position in which it usually occurs as being the same as those surrounding ectoparasitic animals generally. I should hardly consider this difference of more significance than the geographical one — one species occurring in N. America and the other in Africa. But, however, that may be I think we can hardly consider differences in habit as having equal systematic value with morphological differences. All that we positively know of the morphology of the two species indicates a very close relationship. The differences which questionably exist are of the nature of at most specific differences. I cannot regard the sum of these as constituting a valid generic distinction. Had MONTICELLI treated LEIDY's genus *Cotylaspis* with as much consideration as KOFOID is inclined to give to MONTICELLI's *Platyaspis* I think we may safely say the latter genus would not have been proposed. KOFOID's rehabilitation of LEIDY's *Cotylaspis* leaves in my opinion, no room for MONTICELLI's *Platyaspis*.

The genus *Stichocotyle* of CUNNINGHAM was refused recognition by MONTICELLI ('92) on the ground that only the larva was known and this might not improbably prove to be the larva of *Macraspis*. Since that time ODHNER ('98) has discovered the adult of *Stichocotyle* and fully established the connection between it and the larval form and also its specific distinctness from *Macraspis*. His observations taken in connection with what was before known concerning the larva (CUNNINGHAM '87, NICKERSON '95) make the life history of this form better known at present than that of any other Aspidobothrid. In my paper (NICKERSON '95) on the larval *Stichocotyle* I suggested the possibility that the adult when found might resemble *Macraspis* sufficiently to warrant the putting of both forms in the same genus. The main facts of the internal anatomy of *Macraspis* have since become known thro' the investigations of OLSSON ('96) and JÄGERSKIÖLD ('99) and although complete descriptions of the adult *Stichocotyle* are not yet published enough is known from the papers mentioned above to warrant the statement that the genus established by CUNNINGHAM should be retained for the latter form. The chief differences between the two genera as far as known at present are:

Macraspis	*Stichocotyle*
Single compound ventral sucker.	Ventral suckers numerous — mostly distinct.
Marginal sense organs present.	Marginal organs lacking.

Macraspis	*Stichocotyle*
Single testis, near posterior end.	Two testes in middle region of body or farther forward.
Ovary far forward.	Ovary in middle region of body or farther forward.
Sexual aperture median.	Sexual aperture on right of median line.

Of the differences mentioned that in the number and position of the testes is doubtless to be regarded as the most important and will probably be found to be accompanied by other differences in the reproductive systems. MONTICELLI's objection to the recognition of the genus *Stichocotyle*, tho' valid when made, can no longer be maintained and the genus is therefore entitled to full recognition.

Family *Aspidobothridae* BURM. 1856.

Body variously shaped, elongated or short, cylindrical or flattened. Ventral surface bearing a large oval or elongated compound adhesive organ composed of numerous alveoli arranged in one or in several rows or the adhesive organ may be represented by a series of numerous simple acetabula in a single longitudinal row. Chitinous hooks or similar structures lacking. Mouth terminal or subterminal not surrounded by an oral sucker. Pharynx present; intestine simple, tubular or saccate, surrounded by a single or double muscular sack developed in the parenchyma; when the sack is double a part of the genitalia lie ventrally between the outer and inner sacks. Single aperture for both male and female genital systems situated in or near the midventral line anterior to the adhesive organ or to the foremost acetabulum. Uterus usually long and tortuous. Ovary of medium size. Testes one or two posterior to ovary. LAURER's canal present or absent. Yolk glands extending for some distance longitudinally near the lateral margins of body either as continuous masses or as numerous separate follicles. Eggs without filaments, usually numerous. Excretory system opening by a dorsal pore near posterior end. Excretory vesicles paired extending forward a longer or shorter distance near each side. Development direct with simple metamorphosis.

Live as parasites in the intestinal tract or gall bladder and bile ducts of fishes and turtles as well as upon the bodies or in various organs of Mollusca.

Table for preliminary determination of genera.

1. Adhesive organ composed of numerous more or less distinct acetabula in a single row. Marginal sense organs lacking. 2 testes *Stichocotyle*
2. Adhesive organ composed of a single row of confluent acetabula. Sense organs present. 1 testis *Macraspis*
3. Adhesive organ elongated composed of 3 rows of alveoli, the median transversely elongated and shallow, the lateral smaller and rounded; mouth terminal surrounded by an expanded buccal disk. Sense organs present. 2 testes *Cotylogaster*
4. Adhesive organ oval or elliptical, composed of 3 rows of alveoli; mouth subterminal not surrounded by buccal disk. Sense organs present. 1 testis *Cotylaspis*
5. Adhesive organ oval, $^2/_3$ length of body, composed of 4 rows of alveoli; mouth subterminal not surrounded by buccal disk. Sense organs present. 1 testis *Aspidogaster*

1. Genus: ***Stichocotyle*** Cunningham 1884.

Literature: Cunningham '84; '87. — Nickerson '95. — Odhner '98.

Body greatly elongated, cylindrical, anterior end flattened dorsoventrally, tapering in posterior third. Ventral side bearing a single longitudinal row of between 20 and 30 transversely elongated acetabula encircling the ventral half of the body. Anterior acetabulum circular, those near posterior end of series smaller and more or less confluent. Sense organs lacking. Mouth subterminal at base of a funnel shaped depression, not surrounded by a distinct sucker. Pharynx medium, intestine simple tubular extending nearly to posterior end of body. Excretory pore dorsal, median, near posterior extremity. Genital aperture anterior to margin of first acetabulum, a little to the right side. Eggs large oval. 2 testes.

Adults live a parasites in the bile passages of the liver of rays; larvae occur encysted in wall of intestine of the larger marine crustacea.

The only species is

S. nephropis Cunn. 1884.

In bile passages of liver of species of *Raja* on coast of Europe and N. America.

2. Genus: *Macraspis* Olsson 1868.

Literature: Braun '89—'93. — Jägerskiöld '99. — Monticelli '92. — Olsson '68; 96.

Body greatly elongated, cylindrical, tapering anteriorly. Adhesive organ covering the ventral surface thro' nearly the entire length of the body, sharply defined; made up of a single row of transversely elongated alveoli. Marginal sense organs present. Mouth terminal, pharynx medium, oesophagus short and muscular, intestine simple, near dorsal surface, reaching nearly to posterior extremity. Genital opening median in the depression at the anterior margin of the ventral adhesive organ. Ovary at beginning of second quarter. Laurer's canal present. Paired vitellary glands in form of continuous elongated cords, placed laterally and extending on each side from region of ovary back nearly to posterior end of body. Vitellary ducts paired. Uterus long: eggs numerous, large, oval. Testis single, large, near posterior end. Penis present.

Live as parasites in the gall bladder of fishes; larva not known.

The only species is

M. elegans Olss. 1868.

In gall bladder of *Chimaera monstrosa* on the coast of Europe.

3. Genus: *Cotylogaster* Mont. 1892.

Literature: Braun '89—'93. — Monticelli '92. — Nickerson '99.

Body in two regions a narrower anterior and a broader posterior portion within which the former may be partially retracted telescopically. Ventral adhesive organ more than half the total length of the body; composed of a single longitudinal row of transversely elongated grooves, which is surrounded by a marginal row of a smaller rounded alveoli. Marginal sense organs present. Mouth near centre of a disk-like expansion of the anterior end. Prepharynx long; pharynx medium. Intestine extending thro' more than $^2/_3$ the length of the body. Genital pore median, ventral, in front of anterior margin of ventral shield. Ovary a little smaller than testes. Uterus long and varicose. Vitellaria laterally placed. Testes 2, posterior to ovary. Musculature forming a double visceral sack.

Live as parasites in the intestine of fishes.

The species are:

C. michaelis Mont. 1892.

In the intestine of *Cantharus vulgaris* (Trieste).

C. occidentalis Nickerson 1899.

In intestine of *Aplodinotus grunniens* (Minnesota River at Jordan).

4. Genus: ***Cotylaspis*** Leidy 1857.

Literature: Kelly '99. — Kofoid '99. — Leidy '57; 58. — Monticelli '92. — Osborn '98. — Poirier '86.

Anterior part of body in the form of a truncated cone set obliquely upon an expanded posterior portion which has a convex dorsal and flattened ventral surface. Body not extending beyond the hinder margin of the ventral shield, which is $^2/_3$ the length of the animal and composed of 3 longitudinal rows of alveoli. Sense organs present (?). Mouth subterminal, pharynx medium, intestine simple, tubular, $^2/_3$ the length of the body. Genital pore median in front of anterior margin of ventral shield. Testis single in posterior portion of body. Ovary on right side, smaller than testis. Uterus only moderately elongated, ova not numerous, large, oval. Vitellaria consisting of numerous follicles laterally placed. Penis present.

Live as parasites in mantle cavity of *Unionidae* and in intestine of turtles.

The species are:

C. insignis Leidy 1857.

In mantle cavity of various species of *Unionidae* in N. America.

C. lenoiri Poir. 1886.

In intestine of *Tetrathyra* from Senegal.

5. Genus: ***Aspidogaster*** v. Baer 1827.

Literature: v. Baer '27. — Diesing '34. — Kelly '99. — Kofoid '99. — Macdonald '78. — Stafford '96. — Voeltzkow '88; 88a.

Body more or less elongated, broader in the middle narrowing anteriorly to the cylindrical neck, pointed posteriorly. Dorsal surface convex. Ventral shield elliptical covering $^2/_3$ or more of the ventral surface. Composed of four rows of rectangular or hexagonal alveoli; margin notched, containing sense organs and in one case provided with retactile tentacles. Mouth terminal, highly distensible. Pharynx usually small. Intestine nearly as long as the body, simple, broadening slightly posteriorly. Sexual aperture median, ventral at base of depression immediately in front of the margin of the ventral sucker. Ovary small; testis single equal in size to ovary. Vitellary glands numerous, laterally placed. Uterus of medium length, ova rather large elliptical.

Live as parasites in pericardium and renal organs of fresh water Lamellibranchs, in intestine of fresh water fishes and in marine Gastropods.

The species are:

A. conchicola v. Baer 1827.

In kidney and pericardium of various species of *Unionidae* of Europe and N. America, in Gastropods; also in immature condition in intestine of *Unionidae.*

A. limacoides Dies. 1834.

In intestine of different species of *Leuciscus* in Europe.

A. macdonaldi Mont. 1891.

In siphon of *Melo* in Australia.

Little is known concerning the species *A. macdonaldi* Mont. It may be considered certain that it is an Aspidobothrid and extremely probable that its nearest affinities are with *Aspidogaster.* Its internal structure is, however, almost entirely unknown. Externally it differs from all other known Aspidobothrids in the possession of tentacles (180 in number according to Macdonald) capable of protrusion and retraction like the tentacles of a snail. It is not improbable that they represent the marginal sense organs of other forms highly modified though they are present not only around the margin of the ventral shield but also in all the intersections of the ridges which separate the different alveoli. It is possible that a new genus may have to be created for this species when its internal structure shall become known.

University of Minnesota, Minneapolis,
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Explanation of Figures.

All the drawings (Figs. 15 and 16 excepted) were made with the aid of an ABBE's camera from specimens of *Cotylogaster occidentalis*.

Abbreviations used:

ac acetabulum	*ov'd't* oviduct
c.f caudal foramen	*p. gl* prostate gland
d.c dorsal cone	*ph* pharynx
ex.t excretory tubule	*pph* prepharynx
ex.v excretory vesicle	*r.s.ut* receptaculum seminis uterinum
g.c gland cell	*s. gl* shell gland
g.p genital pore	*s.p* sense papilla
in intestine	*s.v* seminal vesicle
L.c LAURER's canal	*tes* testis
m mouth	*v.d* vas deferens
m.o marginal sense organs	*vit.d* vitelline duct
n nucleus	*vit. gl* vitelline gland
o ova	*ut* uterus
ov ovary	

Plate 32.

Fig. 1. Lateral view of an entire alcoholic specimen in which the anterior portion is retracted. 17 : 1.

Fig. 2. Anterior portion of a similar specimen in which the anterior portion is fully protruded. 17 : 1.

Fig. 3. Anterior portion of another specimen in lateral view. 17 : 1.

Fig. 4. Same specimen in ventral view. 17 : 1.

Fig. 5. Oblique dorsal view of posterior portion of a specimen. 17 : 1.

Fig. 6. View of tip of dorsal lobe of oral disk as seen in entire preparation showing sensory (?) papilla. 250 : 1.

Fig. 7. Median sagittal section of specimen from which Figs. 3 and 4 were drawn. 22 : 1.

Plate 33.

Fig. 8. Transverse section of "neck" anterior to pharynx. 57 : 1.

Fig. 9. Transverse section through anterior edge of ventral shield showing embryos in sulcus at base of neck. 22 : 1.

Fig. 10. Transverse section through ovary and anterior testis. 22 : 1.

Fig. 11. Longitudinal section of marginal sense organ. 675 : 1.

Fig. 12. Similar section of another sense organ. 675 : 1.

Fig. 13. Section of marginal sense organ in protruded state. 675 : 1.

Fig. 14. Longitudinal section of a sense organ showing course of duct to exterior. 675 : 1.

Fig. 15. Diagram showing relations of organs in *C. occidentalis* as seen from dorsal side, the animal being represented as straightened horizontally with the dorsal cone projected backward. Outlines of animal (including ventral sucker), intestinal tract and excretory system (so far as shown) in black; sexual organs in red; vitellary glands and duct and LAURER'S canal in brown.

Fig. 16. Diagram to show relations of parts in intimate connection with ovary as they would be seen from ventral side.

Fig. 17. Longitudinal nearly sagittal section of an embryo of *C. occidentalis* soon after leaving the egg. 680 : 1.

Fig. 18. Posterior half of section next following the one represented in Fig. 17. 680 : 1.

Fig. 19. Drawing made by combining parts of two adjacent nearly transverse sections of an embryo through region of pharynx and anterior band of cilia. 680 : 1.

Fig. 20. Surface view of tuft of cilia as seen in tangential section. 1220 : 1.

Fig. 21. Nearly sagittal section of anterior end of an embryo showing gland cell (spine gland). 680 : 1.